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THE ALLIUM AMPELOPRASUM COMPLEX ON CRETE

by

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ABSTRACT

The variation in the *Allium ampeloprasum* complex on Crete is presented. A new, tetraploid ($2n = 4x = 32$) subspecies, endemic to Crete is described: *Allium bourgeaui* Rech. fil. subsp. *creticum* Bothmer. Chromosome numbers and data of reproductive pattern of the species present on Crete are given.

INTRODUCTION

The account, published in 1974 (BOTHMER 1974), at the morphological and cytological variation of the *Allium ampeloprasum* complex on the East Mediterranean island of Crete was necessarily in some respects preliminary; much more material has now become available and provides the basis for a needed revision.

Two series of forms were described there from Crete, one chasmophytic, i. e. growing on cliffs and steep rocky slopes, and the other ruderal, i. e. growing on roadsides, the edges of fields and in cultivated land, both, however, being referred to *A. ampeloprasum* L. mainly because of their tepal papillation. *A. bourgeaui* Rech. fil. and *A. commutatum* Guss. were also recorded from Crete.

The present study aims to evaluate the taxonomic status and the variation of the chasmophytic series and to indicate its relationship to other members of the group. Morphological variation within the field and ruderal populations has likewise been examined, since deviating types frequently occur. For comparison with populations outside Crete, the chromosome numbers of all living Cretan material available determined. Different levels of ploidy are known

in *A. ampeloprasum* from other areas while diploids predominate in *A. bourgeaui*, thus the conditions on Crete have had to be clarified. In order to visualize possible chromosome morphological differences, the karyotypes from some populations were investigated. It had already been found that reproductive pattern can give information with taxonomic implications as also about differentiation pattern (BOTHMER 1974); thus on investigation of this in Cretan material was undertaken to evaluate similarities with material elsewhere.

MATERIAL AND METHODS

Most of the material studied for the present paper was collected by the author in 1974 and cultivated in the Botanical Gardens of Munich and Lund. For determination of chromosome numbers 92 plants from 40 populations were used. Localities of all studied populations are given in an appendix.

For chromosome studies the usual Feulgen-squash technique was used (see BOTHMER 1970) with pretreatment of a mixture of 0,5 % colchicine and 2 mM 8-hydroxyquinoline for 2,5 hours. Staining with cotton blue was used for pollen fertility studies, and 400 pollen grains per plant were counted.

ALLIUM AMPELOPRASUM

A. ampeloprasum L. s. str. is fairly homogeneous in the region from Italy to Turkey, but it shows a great morphological variation with local forms occurring on Crete not met with outside the island. It relates to some extent to the occurrence of different levels of ploidy (Fig. 4), but there is no distinct correlation between morphology and chromosome numbers. Most pentaploid populations, which are also the most common ones (Fig. 4), show in general a good morphological coincidence. Tetra- as well as hexaploid populations are very diverse inter se, but the two heptaploid populations on NW Crete are similar. Two of the three hexaploid populations, one from W and one from E Crete have very long tepals and pistils in common, but are otherwise rather dissimilar (Fig. 2).

The populations on mid-Crete, which are mainly pentaploid, show a rather small range of variation and coincide morphologically with the forms found in other areas in Greece (BOTHMER 1974). The inflorescences are 5.5 to 7.5 cm in diameter, spathes c. 10 cm long, bulbils 6-10 mm long. flower colour white or pale pink to red. Papillation of tepals is that typical for *A. ampelo-*

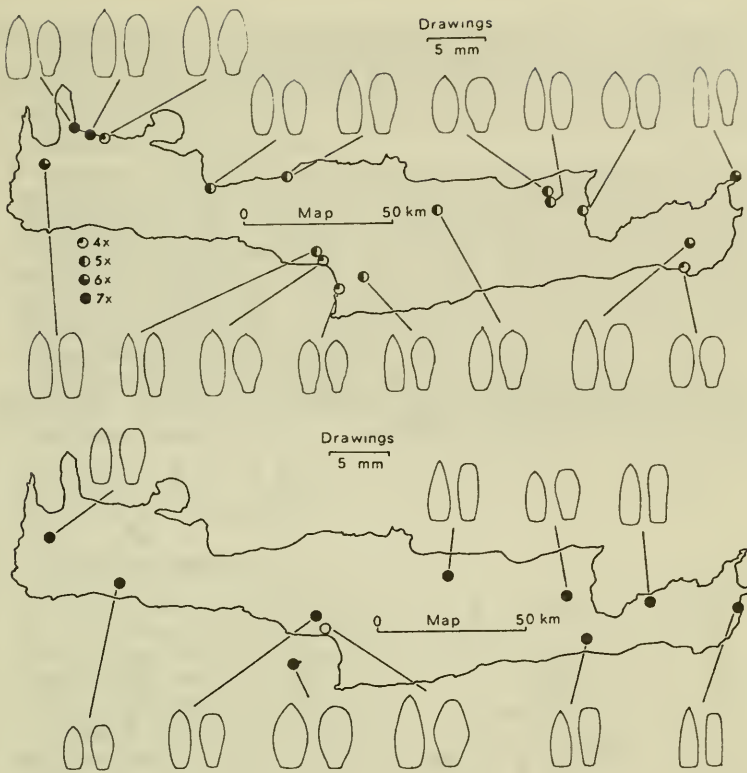


Fig. 1. Variation in shape of tepals. - Top: *Allium ampeloprasum*. - Bottom: *A. bourgeaui* (dots) and *A. commutatum* (ring). Each population is represented by (from left) one outer and one inner tepal.

prasum , i.e. large, longish papillae in rows, especially around the mid-vein. The flat part of the filament has a rounded outline. The shape of the tepals varies for example from mucronate to non-mucronate (Fig. 1), but not more so than in other areas in Greece.

Four populations from mid-Crete are, however, deviating. In the pentaploid population B 866 (NW of Ag. Galini) the plants are very stout, with very long spathes (c. 20 cm) and narrow tepals (Fig. 1). Populations B 848 (at Ag. Nikolaos) and B 865 (NW of Spili), both pentaploid, have tepals more or less densely covered with small papillae and have also very large bulbils (up to 20 mm long). The tetraploid population B 869 (at Matala) is very small-grown, with inflorescences 2.5-3.5 cm in diameter, bulbils 3-4 mm long, small tepals, the outer whorl of which having a quite peculiar shape, similar to that of inner tepals (Fig. 1). The tepals are smooth or have low ridges.

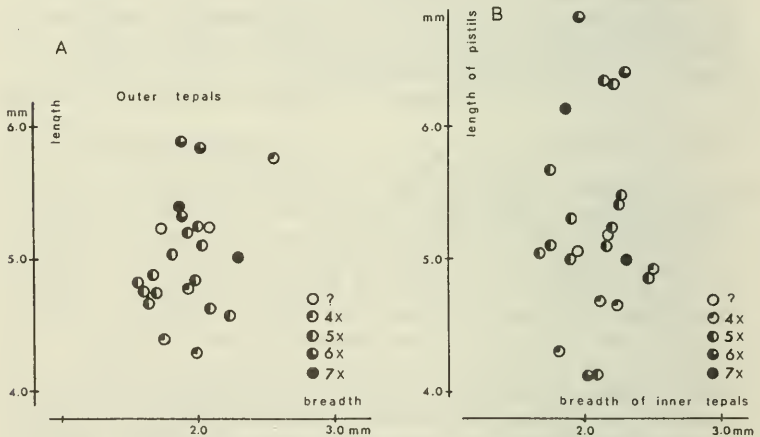


Fig. 2. Allium ampeloprasum. Intrapopulation variation in some floral characters. Each symbol represents the mean for one population.

On E Crete only three populations of *A. ampeloprasum* have been found, one tetra- and two hexaploid ones, of which the

latter ones are somewhat outstanding. Population S, B & ST. 21045 (Kap Sidero) has very narrow tepals (Fig. 1) and short pistils (Fig. 2). Population B 854 (at Sikia) agrees morphologically with other representatives of *A. ampeloprasum*, but has very long pistils and tepals (Fig. 2).

The *A. ampeloprasum* material from NW Crete is rather polymorphic, and includes different degrees of polyploidy, 4 x up to 7 x (Fig. 4). Common to all investigated material is the stout habit (the plants are up to 2 m high) and large inflorescences (5-10 cm in diameter). Most populations have large, longely mucronate outer tepals (Fig. 1). There is also a considerable variation in size of tepals and length of pistils (Fig. 2). Population B 42 (W of Chania) deviates in papillation by having the tepal surface covered with small or medium-sized, conical papillae. In some of the plants in population B 859 (W of Chania) bulbils upgrown on the scape was observed. This condition has previously not been found in any other material of the *A. ampeloprasum* complex but is common in *A. sphaerocephalum* L. and *A. amethystinum* Tausch.

ALLIUM BOURGEAUUI

In the large gorge systems of Crete a representative of the *A. ampeloprasum* complex is common, often in big populations with over 1000 individuals. Two of these cliff populations from eastern Crete were referred to *A. bourgeaui* Rech. fil. subsp. *bourgeaui* by BOTHMER (1974), who stated, however, that they deviated morphologically from the Rodhos-Karpathos material of this taxon. The rest of the cliff populations were classified as a chasmophytic form of *A. ampeloprasum*, due to the presence of big papillae on the abaxial surface of the tepals. However, after investigations of more material it is clear that most cliff populations on Crete must be referred to *A. bourgeaui* due to the presence of the following characters: few, big bulbils, long protruding stamens, the outer whorl of which is simple, narrow inner tepals and outer tepals that are usually broadest at base. The chasmophytic habitat is also connecting the Cretean populations to the other two subspecies of *A. bourgeaui*. There are, however, so great morphological differences from subsp. *bourgeaui* and to subsp. *cycladicum*, which justify the description of a new taxon.

Allium bourgeaui Rech. fil. subspecies *creticum*
Bothmer, subspecies *nova*

Orig. coll.: Greece, Nomos Lasithion, Epirus Sitia, 1 km SSW of Tourloti; in NW-exposed limestone cliff, c. 200 m s.m. Leg. R. von BOTHMER, no B 857, 22. 5. 1974 (LD holotype).

Diagnosis: Differt a subspecie *bourgeaui* floribus roseis ellipsoideis vel ovoideis, tepalis interioribus plerumque spathulatis, tepalis omnibus facie dorsali papillis magnis parvisque mixtis obtectis.

Description:

Scape (49-) 60-115 cm long; leaf sheaths covering $1/3-1/2$ (- $2/3$) of the scape. - Renewal bulb ovoid; protective layer thick, sclerified, greyish-brown to brown, membranaceous; inner tunics white, membranaceous. - Bulbils 0-4, situated around the renewal bulb, ovoid, with an acute apex, semi-circular in transection, 9.5-14 (-23) mm long, (7-) 8-12 (-15.5) mm broad; protective layer double, both coats yellowish-brown to brown. - Leaves 5-9 (-11) per scape, withered at the time of flowering; the uppermost (= narrowest) leaf 0.9-1.4 cm broad; the broadest leaf (1.3-) 1.6-2.0 (-2.5) cm broad; flat, carinate, margin and keel scabrous; leaf sheaths at base not becoming fibrous. - Ligule (1.2-) 1.6-3.0 mm long. - Spathe univalvate, early deciduous, 5-12 (-16) cm long. - Inflorescence hemispherical to globose, (4.0-) 4.8-6.2 (-7.0) cm in diameter. - Flowers ellipsoid rarely ovoid pink to red. - Outer tepals (3.8-) 4.0-5.2 (-6.0) mm long, (1.2-) 1.4-2.0 (-2.8) mm broad, broadest below the middle, rarely at the middle, with mucronate or obtuse apex; abaxial surface covered with small papillae and some big papillae in rows around the mid-vein. - Inner tepals (3.8-) 4.0-5.0 (-5.6) mm long, (1.2-) 1.4-2.0 (-2.9) mm broad, usually somewhat shorter than the outer tepals, spathulate to uniformly broad; apex truncate, rarely slightly emarginate; abaxial surface covered with small papillae and rarely some larger papillae and rarely some larger papillae around the midvein. - Filaments (3.7-) 4.3-5.3 (-6.1) mm long; the two whorls equal in size and longer than the tepals. Outer filaments simple, rarely with minute lateral cusps, 0.7-1.4 mm broad; flat part of the filament + uniformly broad. Inner filaments tricuspidate, 1.6-2.1 (-2.6) mm broad; flat part of the filament uniformly broad or somewhat elliptical; lateral appendages up to c. 5 mm long. - Anthers yellow

ssp.	Scope (cm)	Bulbil length (cm)	Number of leaves	Spathe (cm)	Inflorescence (cm)	Flower colour
<u>ssp. bourgeaui</u>	45-90	8-16	4-11	8-17	3, 0-5, 0	whitish green
<u>ssp. cycladicum</u>	45-100	7-16	4-8	5-14	3, 0-5, 8	purple
<u>ssp. creticum</u>	60-115	9-14	5-11	6-12	4, 8-6, 2	pink to red

	Length of outer tepals (mm)	Breadth of outer tepals (mm)	Pistil (mm)	Length of seeds (mm)	2n
<u>ssp. bourgeaui</u>	2, 5-4, 0	0, 9-1, 5	3, 5-5, 0	2, 2-3, 4	2 x
<u>ssp. cycladicum</u>	2, 5-4, 0	0, 8-1, 6	3, 8-5, 1	2, 3-3, 4	2 x, 3 x, (4 x)
<u>ssp. creticum</u>	4, 0-5, 2	1, 4-2, 0	4, 7-5, 7	3, 0-4, 2	4 x, (5 x)

Table 1. A. comparison of some characters between the subspecies in *Allium bourgeaui* Rech. fil. All extreme values are omitted.

to red, rarely purple. - Pistil (4.1-) 4.7-5.7 (-6.0) mm long.
- Capsule valves + orbicular, (2.9-) 3.5-4.5 (-5.0) mm in diameter. - Seeds (2.7-) 3.0-4.2 mm long, (1.5-) 1.7-2.2 (-2.7) mm broad, triquetrous. - Chromosome number $2n = 32$.

A. bourgeaui subsp. *creticum* is best characterized by the presence of both big and small papillae on the tepals, the red flower colour, and the usually spatulate inner tepals.

Subsp. *creticum* differs conspicuously from both subsp. *bourgeaui* and subsp. *cycladicum* by its stouter habit, usually bigger inflorescences, longer and broader tepals and stamens, more narrow capsule valves, and a different flower shape. The other two subspecies have campanulate to cylindrical flowers whereas subsp. *creticum* has ellipsoid ones. There are also differences in flower colour and tepal papillation (see below). A comparison between the three subspecies within *A. bourgeaui* is presented in table 1.

Distribution: see Fig. 4.

Habitat: The plants of *A. bourgeaui* subsp. *creticum* are mostly inhabiting steep limestone cliffs, often in the big ravines and gorges on Crete. They are usually growing in more inaccessible sites than subsp. *bourgeaui*. Three inaccessible populations certainly belonging to this taxon were seen by the author in 1974 (at Langada, at Kandanos, and at Zaros).

Flowering period: mid June - July.

Variation: The studied material of *A. bourgeaui* subsp. *creticum* is rather homogeneous but with some populations which are morphologically somewhat deviating. Population S, B & ST 20908 from Paximadia major, a small island S of Crete is especially outstanding in most characters (Figs. 1, 3).

Vegetative characters: The plants are generally tall-grown, with broad leaves, the number of which can vary considerably (from 5 to 10 was found in one population). Characteristic is the relatively short spathe, which rarely exceeds 12 cm. Sometimes the pedicels bend upwards in fruiting stage, a trait which is normally characteristic for *A. commutatum*.

Bulbils: The bulbils display a rather large variation in both size and shape. The single diploid population found on Crete, B 864 (at Paleochora), the bulbils are long, narrow and acuminate and with a papillate surface. This bulbil shape does not agree with the

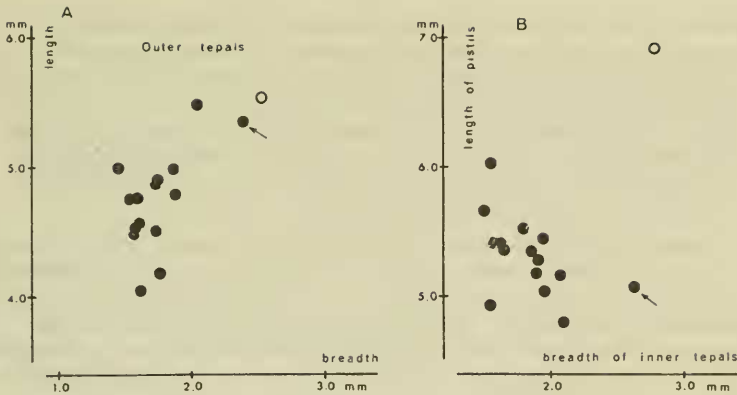


Fig. 3. *Allium bourgeauii* (dots) and *A. commutatum* (ring). Variation in some floral characters. Each symbol represents the mean for one population. Arrow indicates population no. S, B & ST20908 (*Paximadia major*).

normal one in *A. bourgeauii*, and since no flowering plants have been examined from it is uncertain if it belongs to subsp. *creticum*.

Flower colour: Common to all Cretean populations are the pale red to red flowers.

Outer tepals: These are in subsp. *creticum* narrow, usually broadest at base, which is a typical trait for *A. bourgeauii*. In some populations, however, they are broadest at the middle. Most plants have shortly mucronate outer tepals. Populations B 850 and B 851 (both at Kritsa) have shorter outer tepals and population R & S 17906 (at Kato Zakros) has longer ones in comparison with the other populations (Fig. 1, 3A).

Inner tepals: One of the main distinguishing characters for *A. bourgeauii* is the presence of short and narrow inner tepals. Most populations on Crete have spatulate tepals but there is a continuous variation to more or less uniformly broad ones in different populations (Fig. 1).

Tepal papillation: Most populations on Crete have the abaxial tepal surface more or less densely covered with low, longish together with a varying number of large papillae in rows, concentrated around the midvein. This type is otherwise present in *A. ampeloprasum*. In populations B 852 and B 889 (both at Kalamafka) is the large type of papillae predominating and in B 46 and B 857 (both at Tourloti) there is a continuous variation from small or intermediate papillae up to large ones.

Stamens: Both outer and inner stamens in subsp. *creticum* are long exserted from the flowers, which is a typical character for *A. bourgeaui* as a whole. The flattened part of the stamen is uniformly broad and rather narrow. In some populations the outer stamens, which are normally simple, are di- or tricuspidate having small lateral appendages, but never the long ones occurring in *A. commutatum*.

Anthers vary from mucronate to non-mucronate in shape and from yellow to red or purple in colour.

Pistils: There is a relatively restricted variation in length of pistils (Fig. 3B).

ALLIUM COMMUTATUM

GANDOGGER (1916) described *A. bimetricale* from Crete, which was considered as an endemic species to the island. It is, however, a synonymous with *A. commutatum* Guss., which has a distribution mainly on small islands in the eastern Mediterranean region. The type collection of *A. bimetricale* from NW Crete (GANDOGGER 4880, LY) contains both true representatives for the species as well as intermediate types to *A. ampeloprasum*. In the material collected by the author one cliff-growing population of *A. commutatum* was found on S Crete (B 867). Some populations of the species on islets close to Crete have already been considered (BOTHMER 1974).

Population B 867 has throughout the morphological traits typical for *A. commutatum*, i. e. tricuspidate outer stamens, broadly spatulate inner tepals and broadly elliptic outer ones (Figs. 1, 3), the tepals are rather hard. The tepal papillation consists of a very dense cover of small, narrowly conical papillae.

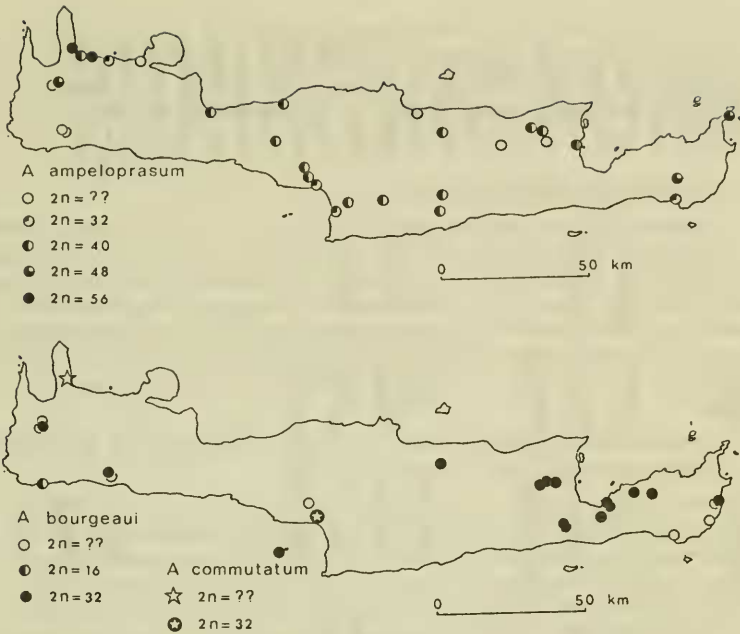


Fig. 4. Distribution of different chromosome numbers in the *Allium ampeloprasum* complex on Crete.

CHROMOSOME NUMBERS AND MORPHOLOGY

Chromosome Numbers (Fig. 4)

In *A. ampeloprasum* is the variation in chromosome numbers considerable. Most common are the pentaploids, ($2n = 5 \times = 40$), which are found all over Crete (in all 14 populations). Tetra- and hexaploid populations ($2n = 4 \times = 32$ and $2n = 6 \times = 48$) have a scattered distribution, and on NW Crete, where the morphological variation is greatest two heptaploid populations ($2n = 7 \times = 56$) have been found.

The cliff populations are throughout very homogeneous as to

chromosome numbers. The single population of *A. commutatum* (B 867) is tetraploid, which is also the case for most material of *A. bourgeaui* subsp. *creticum* (15 populations). One single cliff population is diploid (B 864, $2n = 2x = 16$).

Chromosome Morphology (Fig. 5)

The karyotypes of the Cretan material are of the same general appearance as was described for the whole *A. ampeloprasum* complex by BOTHMER (1970), with no special characteristics for the different taxa. The chromosome complement is symmetrical with mainly metacentric chromosomes and with continuous transition in size, which removes the possibility of an individual recognition of the chromosome pairs. The karyological variation is also very small.

The marker chromosomes are easily detectable with secondary constrictions and large linear satellites.

The single submetacentric pair, no. 8 (armindex 2.0-3.0) is of the so called *scorodoprasum* type (VED BRAT 1965) with short arm and satellite of similar length. In some cases is no secondary constriction visible, but the chromosome can always be identified due to the submetacentric condition, then called 8- (cf. BOTHMER 1975). The satellite has often a faint secondary constriction in about median position (Fig. 5 E).

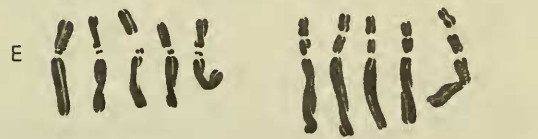
Chromosome pair no. 7 is of *neapolitanum* type (VED BRAT op. cit.), with a minute short arm and a long segment defined as satellite. Sometimes the constriction is invisible (7-) and the chromosome cannot then be identified due to its similarity to the rest of the homomorphic complement.

In a few cases a secondary constriction is present in chromosome no. 6, of *sativum* type (VED BRAT op. cit.), with the

Fig. 5. Karyotype and marker chromosomes of some populations in the *Allium ampeloprasum* complex on Crete. - A-C: *Allium bourgeaui* ssp. *creticum*. - D-G: *A. ampeloprasum*. - A, C: Pop. no. B 874, 4x. A showing the non-marker chromosomes. - B: Pop. no. B 864, 2x. - D: Pop. no. B 859, 4x. - E: Pop. no. 871, 5x. - F: Pop. no. B 862, 6x. - G: Pop. no. B 861, 7x.



0 10 μ



satellite somewhat longer than the short arm. This chromosomal type is, however, never present in maximal numbers (e.g. four in tetraploids).

In some populations secondary constrictions and satellites are present, of types that have not been found previously in the *A. ampeloprasum* complex (Fig. 5 D, G) designated with question marks).

No B chromosomes have been observed in the material from Crete.

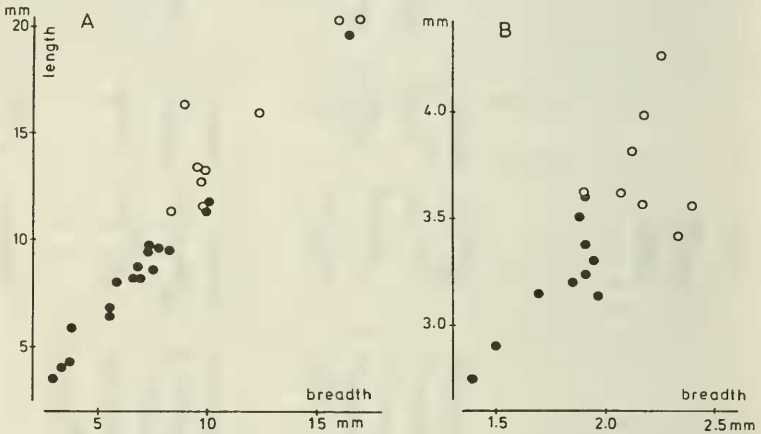


Fig. 6. Intrapopulation variation in size of - A: Bulbils. - B: Seed. Dots: *Allium ampeloprasum*; Rings: *A. bourgeaui*. Each symbol represents the mean for one population.

REPRODUCTION

The data of reproductive pattern of the taxa in the *Allium ampeloprasum* complex on Crete coincide well with those results obtained from other areas in the Aegean (cf. BOTHMER 1974).

Pollen stainability (Table 2). In *A. ampeloprasum* there is a wide variation between populations. Three of the four tetraploids have rather good pollen, but the fourth (B 869, from

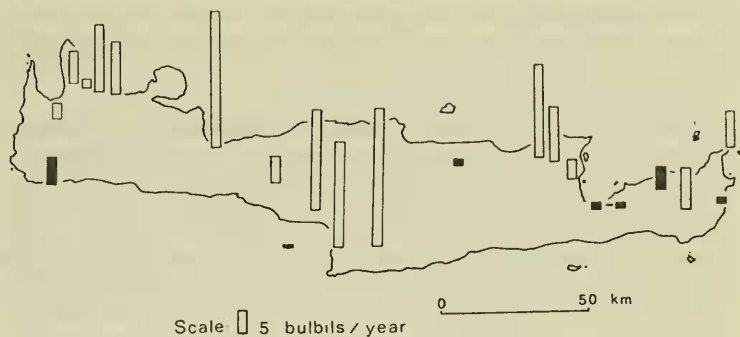


Fig. 7. Variation in bulbil production. White histograms: *Allium ampeloprasum*; Black histograms: *A. bourgeaui*. Each histogram represents the mean for one population.

mid-Crete) has low values. The rest of the populations with higher degree of polyploidy have throughout bad pollen formation, with e. g. 9 populations with less than 15 % good pollen. A few of the pentaploids have, however, up to 70 % good pollen.

	0	50	60	70	80	90	100 %	populations
<u><i>A. ampeloprasum</i></u>	16	1	1	3	1	3		25
<u><i>A. bourgeaui</i></u>						6	8	14
<u><i>A. commutatum</i></u>	1							1

Table 2. Variation in pollen stainability (% good pollen) in different populations in the *Allium ampeloprasum* complex on Crete.

A. bourgeaui subsp. *creticum* has throughout high pollen stainability values (>85 %). The single studied population of *A. commutatum* (B 867) has extraordinarily bad pollen (<10 %).

Seeds and bulbils. The chasmophytic populations have in general larger both seeds and bulbils than *A. ampeloprasum*. However, some of the morphologically deviating populations of the latter species form very large diaspores (Fig. 6).

The asexual reproduction is defined as production of bulbils/year and was calculated as mean values for the populations by determining the number of bulbils produced per year per plant. It shows a very large variation (Fig. 7). Populations of *A. ampeloprasum* on E and W Crete have a comparatively low bulbil production, but the bulbils formed are larger than in the common types of the species. The populations from mid-Crete produce between 20 and 30 bulbils/year, which is somewhat higher than in other areas in the Aegean.

In *A. bourgeaui* subsp. *creticum* the bulbil production is normally low ($<1,5$ bulbils/year). However, population B 856 (from E Crete) produces c. 5,0 bulbils/year and the single diploid chasmophytic population B 864 forms 6,0 bulbils/year.

In some populations of subsp. *creticum* sister bulb formation without flowering has been observed, a feature which is regular in *A. bourgeaui* subsp. *bourgeaui* (cf. BOTHMER 1974).

DISCUSSION

Allium ampeloprasum

On the island of Crete the different populations of *A. ampeloprasum* s. str. are morphologically very diverse. Most of the material of the species from mid-Crete agrees morphologically and as to reproductive pattern to that in other areas in NE Mediterranean. There is also a coincidence in biotope, i. e. that these weedy types are inhabiting disturbed areas, as for example open fields, vineyards and roadsides. On Crete the weedy type on the pentaploid level has been the most successful one.

The populations on W and some on E Crete deviate as to morphology and reproductive pattern and have also a larger variation in chromosome numbers. These populations occur in somewhat more natural habitats, as rocky phrygana, at cliffs, and in a denser vegetation than the normal type. The data of reproductive pattern especially indicate that these populations are adapted to somewhat different habitats. Normally the plants of *A. ampeloprasum* produce numerous, very small bulbils but in these populations there is a production of rather few, but big and heavy bulbils, which

content more nutriments. These bigger bulbils produce stouter sprouts and are thus better fitted for competition in a more or less closed vegetation.

As an interpretation of the relationship between the two types the following hypothesis is put forward. The deviating populations on W and E Crete constitute a more ancient form, which is indigenous to the island. It was earlier common in former natural vegetation and the present populations could be the rest of an earlier larger distribution area. The pure weedy form could have been differentiated on Crete from this more natural form by an alteration of the reproductive pattern to be better adapted to the more open biotopes, which were created through human activity. It could then have been rapidly spread by man to other areas.

The polymorphic and deviating population B 865 is referred to *A. ampeloprasum* due to habit, form of tepals and stamens and shape of bulbils. Some characters are, however, typical for *A. bourgeaui*. The population grew at the base of a cliff and below the cliff, which is low and not comparable to the very big and steep ones where subsp. *creticum* normally is found. It is possible that this population constitutes a hybrid derivative between the two species adapted to an intermediate biotope.

Allium bourgeaui

The endemic taxon on Crete, *A. bourgeaui* subsp. *creticum* is morphologically distinct and is throughout tetraploid. It is, however, connected to the other two subspecies of *A. bourgeaui* by its distribution and chasmophytic habitat. In comparison with subsp. *cycladicum* it inhabits more extreme cliff areas, and in this respect resembles subsp. *bourgeaui*. On Crete the tetraploid level has been evolved and there is no regional differentiation. The populations are scattered over the island in suitable cliff biotopes. Since cliff systems are common on Crete, different populations and sub-populations have had the possibility of genetic exchange. This has certainly acted against an effect of isolation between different areas on Crete, which is common in other plant groups (GREUTER 1970, 1971). The single population of subsp. *creticum* growing outside the main island of Crete (on the small island of Paximadia major) is also the only one that is morphologically outstanding. It seems plausible to assume that the genetical isolation to other populations has caused a special evolutionary trend and could be a result of random fixation. The single diploid population in the group found on Crete deviates

vegetatively, but since no flowers have been examined its systematic position can not be clarified at present.

The data of reproductive pattern found in subsp. *creticum*, i. e. a high pollen stainability and good seed-setting combined with normally low bulbil production and sister-bulb formation without flowering, coincide with those found in subsp. *bourgeaui*. The versatile reproductive system in the plant group indicates that this similarity is due not to a close phylogenetic relationship between the two forms but rather to the fact that they inhabit similar biotopes. One can assume that the selective forces acting in the chasmophytic habitat have worked to modify the reproductive systems of the two forms in similar directions. As an indication it can also be mentioned that subsp. *cycladicum*, which inhabits a somewhat different type of biotopes, where probably other types of selective forces are operating, shows a partly different reproductive pattern (see BOTHMER 1974).

The three infraspecific taxa of *A. bourgeaui* are distributed around the ancient, very deep Sea of Crete, subsp. *creticum* in S, subsp. *bourgeaui* in SE and subsp. *cycladicum* in N and W (5 populations have recently been found on E Peloponnisos). Due to the old geographical isolation of the area the isolation of the three forms probably lies in Pliocene (see e. g. SNOGERUP 1967, for a discussion of the paleogeography in the area).

Judging from variation pattern subsp. *bourgeaui* seems to be the most ancient form, which is also throughout diploid. It is plausible to assume that radiation has occurred from somewhere in the SE Aegean region. From this diploid ancestor a purely tetraploid form was differentiated on Crete and a di- and triploid one on the Cyclades.

As another explanation, which, however, at present seems more unlikely is that subsp. *creticum* was differentiated from subsp. *cycladicum*, and Crete was probably in this case populated from W.

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APPENDIX. LIST OF LOCALITIES

The following abbreviations of collectors names are used: B=R.
von BOTHMER, G=M. GUSTAFSSON, R=H. RUNEMARK, S=S.
SNOGERUP, ST=A. STRID (all material collected by these persons
is kept in Lund, LD), RECH=K. -H. RECHINGER FIL., Wien (W),
GREUT=W. GREUTER, Geneva (private herbarium), HMG=The
GOULANDRIS collections in the GOULIMI-GOULANDRIS Herbarium
at the GOULANDRIS Natural Museum, Kifissia, Greece.

The geographical subdivision is according to P. T. COUVELIS
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Asterisks indicate non-pressed material (the plants are in
cultivation).

A. AMPELOPRASUM

NOMOS CANEA. Epirus Kissamos. B 860: 0.5 km W of

Tavronitis (20 km W of Chania), c. 10 m; B 861: c. 1 km S of the monastery of Gonia (20 km W of Kastelli); B 862: 1-2 km N of Topolia (10 km SE of Kastelli). - Epirus Selinos. RECH 13616: Supra Kandanos, c. 500 m; RECH 13452: Prope Kandanos, c. 500 m. - Epirus Kidonia. B 42: 23 km W of Chania; B 859: c. 2 km E of Gerani (c. 12 km W of Chania), c. 10 m; HMG 313: Parsiario, 100 m.

NOMOS RETHYMN. Epirus Rethymni. ST 23286: c. 3 km NNE of Pigi, c. 30 m; B 858: c. 3,5 km NNE of Pigi, c. 10 m. - Epirus Ag. Vasilis. B 865: c. 17 km NW of Spili, 360 m; B 866: at the village of Melambes, c. 490 m; S, B & ST 37: 3-4 km NW of Ag. Galini, c. 200 m; S, B & ST 36: 1 km NW of Ag. Galini, c. 100 m.

NOMOS IRAKLION. Epirus Pirgiotissi. B 868: c. 1 km N of Festos, 20-30 m; B 869: 3 km NE of Matala (S of Timbaki), c. 20 m. - Epirus Kinorgyo. B 870: 0.5 km N of Amelouzos (E of Mires), c. 110 m. - Epirus Monofatsio. B 871: c. 2 km N of Pargos; B. 872: 2 km N of Ligortinos, 410 m. - Epirus Temenous. HMG 159: Ag. Irini. - Epirus Padiados. B 873: in the village of Kounavi.

NOMOS LASITHION. Epirus Lasithion. B 52: 2 km SW of Lagnion. - Epirus Mirabello. ST 23285: 1.5 km NW of Latsida, c. 310 m; B 846: 1.5 km NW of Latsida, c. 300 m; B 847: 3 km SE of Neapolis; B 848: Xirokampos, 2-3 km NW of Ag. Nikolaos, c. 40 m. - Epirus Ierapetra. GREUT 7613: Prope Ag. Ioannis. - Epirus Sitia. B 853: Between Perivolakia and Moni Kapsa, c. 100 m; B 854: 1 km W of Sikia (c. 20 km SSW of Sitia); S, B & ST 21045: Kap Sidero, c. 60 m.

A. BOURGEAUI subsp. CRETICUM

NOMOS CANEA. Epirus Kissamos. GREUT⁺ 4679: sdl. Topolia, 250 m; ST 31011: c. 2 km S of Topolia; B 824⁺ (coll. G): S of Topolia; B 863: c. 2 km S of Topolia, 200-250 m. - Epirus Selinos. B 864⁺: 2 km W of Paleochora, c. 100 m (systematical position of this population uncertain). - Epirus Sphakia. RECH⁺ 13775: Levka Ori, inter Samaria et Rumeli, c. 200-300 m; B 825⁺ (coll. G): The gorge of Samaria.

NOMOS RETHYMN. Epirus Ag. Vasilis. S, B & ST 20908: Paximadia islands, the western island; S, B & ST 20960: 1 km N Kriavrissi.

NOMOS IRAKLION. Epirus Temenous. B 874: c. 3 km SW of Archanes, 400-450 m.

NOMOS LASITHION. Epirus Mirabello. B 850: c. 3 km W of Kritsa, c. 400 m; B 851: c. 0.5 km W of Pergiolissia (c. 3.5 km W of Kritsa), 450-500 m; B 888 (coll. S): at Kritsa. - Epirus Ierapetra. B 852: c. 3 km W of Kalamafka, 500 m; B 889 (coll. S): at Kalamafka; B 849⁺: Between Pachia Amos and Monastirakion, 220-280 m; S, B & ST 21040: 1 km SSE of Kavousi, c. 100 m; B 826 (coll. G): at Kavousi. - Epirus Sitia. B 46: 1 km SSW of Tourloti, c. 250 m; B 857: 1 km SSW of Tourloti, 200 m; B 856⁺: Between Achladia and Paraspori, c. 300 m; R & S 18517: Between Achladia and Paraspori, c. 200 m; GREUT 4732: S von Kato Perivlakia bei Kloster Ag. Ioannis Kapsas, 20 m; GREUT 4485: zw. Epáno und Kato Zakros; R & S 17906: The village N of Kato Zakros; B 855: 2.5-3 km SE of Zakros, 30-100 m.

A. COMMUTATUM

NOMOS CANEA. Epirus Kissamos. GANDOGER 4880: Gonia (herb. LY).

NOMOS RETHYMNI. Epirus Ag. Vasilis. B 867: 2-3 km NW of Ag. Galini, c. 110 m.